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Cotton Seedling Abrasion and Recovery from Wind Blown Sand

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ABSTRACT

Millions of hectares of crops are exposed to wind blown sand abrasion each year, and in many instances the damage is thought to be severe enough to require replanting. The goal of this study was to determine the effects of wind blown sand abrasion duration on cotton (*Gossypium hirsutum* L.) seedlings. Seedlings of three cotton cultivars were exposed to wind velocities of 13.4 m s^{-1} with sand abrasive flux density of 0.42 g cm^{-1} width s^{-1} for six treatment durations ranging from 0 to 40 min. Plants were destructively sampled at the time of the sand abrasion treatment and also at ≈2 and 4 wk after exposure. These three sampling dates provided two time intervals for assessing the amount of plant damage and regrowth using classical growth analysis. With increasing sand abrasion treatment time, leaf area and leaf, stem, and total shoot biomass were all reduced while final number of mainstem nodes increased ($P \leq 0.05$). Cultivar differences in leaf mass were significant only at the second destructive sampling date ($P \leq 0.05$). For the first harvest interval, between the first and second destructive sampling, shoot relative growth rate (RGR) and net assimilation rate (NAR) decreased with increasing sand abrasion treatment time. Regrowth during the second harvest interval revealed the opposite pattern, with RGR and NAR both increasing with increasing sand abrasion treatment time. In both harvest intervals, variation in RGR depended mainly on NAR rather than leaf area ratio (LAR). These results indicate that, despite near-complete defoliation at the longest treatment duration of 40 min, cotton plants receiving this level of damage in the field may not require replanting.

Millions of hectares of crops are subjected annually to windblown soil particle abrasion. The resulting injury reduces survival, growth, yield, and quality of both field crops (Adriano et al., 1969; Armbrust, 1968, 1972, 1979, 1982; Armbrust et al., 1974) and vegetables (Armbrust et al., 1969; Skidmore, 1966). Major factors that influence the severity of injury caused by soil abrasion include wind speed (Lyles and Woodruff, 1960), soil particle flux density (Fryrear et al., 1973), and the duration of exposure (Skidmore, 1966). The extent of injury also depends on crop species (Downes et al., 1977), seedling growth stage (Armbrust, 1984), and other environmental factors such as soil moisture content (Fryrear, 1971). Soil particle saltation depends on a number of factors, including wind velocity, surface roughness, and particle size distribution (Merrill et al., 1999; Zobeck and Van Pelt, 2006). In West Texas, minimum wind velocity threshold for saltation is often ≈10 to 13 m s^{-1} (Stout and Zobeck, 1997; Zobeck and Van Pelt, 2006), while wind speeds of 11 to 18 m s^{-1} during dust storms are not uncommon (Ted Zobeck, 2006, personal communication). Following dust storms, farm managers are often faced with the question of whether or not it is economically profitable to replant the crop (Fryrear, 1973).

The reduced growth of sandblasted plants has been attributed to loss of viable leaf tissue, reduced whole plant photosynthesis, increased respiration rates, and possibly short-term high intensity moisture stress due to abraded cuticle and/or impaired stomatal control (Armbrust et al., 1974; Fryrear et al., 1975; Armbrust, 1982). On the other hand, some studies have shown that small amounts of sand abrasion can actually stimulate growth compared with untreated controls (Armbrust, 1968, 1982). Reviewing the literature on moderate wind stress damage and partial defoliation experiments, Grace (1977) concluded that, in some cases, plants can tolerate and even benefit from partial loss of leaf area that may occur through herbivore pressure or wind action so long as the damage does not seriously impact plant water relations over long periods. The objective of this paper was to utilize classical growth analysis to determine the amount of injury and subsequent regrowth of cotton seedlings exposed to a range of sand abrasion duration treatments. A secondary objective was to determine if gross morphological features among cotton cultivars in the form of normal vs. okra leaf shape might confer either resistance to, or recovery from, sand abrasion.

MATERIALS AND METHODS

Plant Culture

Three cotton cultivars FM 832, FM 989, and FM 5013 were seeded into 100 1.7-L pots filled with artificial media consisting of sphagnum peat and medium-grade vermiculite (Sunshine Professional Growing Mix No. 1, Sungro Horticulture Inc., Bellevue, WA)[1] in a greenhouse. Following emergence, plants were thinned to one plant pot^{-1}, and 52 pots $cultivar^{-1}$ were selected for these experiments based on plant uniformity. Pots were irrigated daily with an automated drip irrigation system and the pots were fertilized once per week with soluble fertilizer (Peters Professional 15–16–17 Peat-Lite Special) at a rate of about 0.1 g pot^{-1}. Light levels inside the greenhouse were measured with a solar pyranometer (LI-190SA, LI-COR, Lincoln, NE) at 1 m above one of the benches containing the plants. To prevent potential photoperiod effects among different experiments, supplemental light was supplied from 0500 to 2000 h with 1000-W metal halide lamps (Sylvania, METALARC model M47R, Sylvania, Danvers, MA) when light levels in the greenhouse fell below 360 w m^{-2}. Air temperatures in the greenhouse were measured with shielded

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[1] Mention of this or other proprietary products is for the convenience of the readers only, and does not constitute endorsement or preferential treatment of these products by USDA-ARS.

Abbreviations: LAR, leaf area ratio; NAR, net assimilation rate; RGR, relative growth rate.

copper-constantan thermocouples, and the data were averaged and recorded each hour. Each cultivar was assigned to one bench within the greenhouse and the cultivars were rotated among benches weekly.

Sand Abrasion Treatments

Cotton plants were grown in the greenhouse, exposed to sand abrasion treatments and then returned to the greenhouse. Sand abrasion treatments were applied using the suction-type laboratory wind tunnel described by Fryrear (1971). The wind tunnel has a test section measuring 0.4 m tall, 0.6 m high, and 2.4 m long with a trap door in the bottom to accommodate two potted plants with the top of the pot level with the wind tunnel floor. Wind velocity was measured at 15 cm above the floor immediately upwind of the plants with a pitot tube and static ports connected to a pressure transducer (Setra, Inc., Model 239, Boxborough, MA). A constant wind velocity of 13.4 m s^{-1} was maintained in the wind tunnel during sand abrasion treatments. A washed sand (Silica Sand No. 3, Oglebay Norton Industrial Sands, Inc., Brady, TX) with a particle size < 0.3 mm was used as the abrasive material. The abrasive flux density was 0.42 g cm^{-1} width s^{-1}. Wind blown sand abrasion treatment durations were 0 (control), 5, 10, 20, 30, and 40 min. The wind speed, abrasive flux density, and time treatments used in this experiment were the approximate midpoint treatments used in previous experiments on other plant species (Armbrust et al., 1974; Fryrear and Downes, 1975; Fryrear, 1986). Eight cotton seedlings from each of the three cultivars were exposed to each sand abrasion treatment time. To treat all the plants in this fashion required about 2.5 d. The entire experiment was repeated four times (Table 1).

Growth Analysis

For each cultivar × abrasion treatment time combination, on three sampling dates, groups of four plants were sampled. The first destructive sampling was collected at the time of the application of the sand abrasion treatment on untreated plants only. Thereafter, at ≈2-wk intervals, the second and third destructive samples were collected. Thus, there were four pots per cultivar sampled on the first sampling date, plus four pots × 6 treatment durations for both second and third sampling dates, yielding a total of 52 pots (i.e., $4 + 4 \times 6 + 4 \times 6 = 52$ pots per cultivar). These three destructive harvests provided two growth intervals for performing growth analysis. The sand abrasion treatments damaged leaves and stems to varying degrees, and resulted in the drying, death, and shedding of leaf material. The 2-wk interval between the first and second sampling dates provided sufficient time for the drying and shedding of damaged leaves along with some regrowth. The second interval, between the second and third sampling dates, consisted of regrowth and recovery of the plants.

For each sampled plant, the number of mainstem nodes were counted acropetally with the cotyledonary node designated Node 0, and the node associated with the first true leaf being Node 1, and so forth. A node was considered to have appeared when its associated leaf exceeded 3 cm in length. Green or living leaves were separated from the shoots (stems plus petioles) and leaf area was measured with a leaf area meter (LI-3100, LI-COR, Lincoln, NE). Dry weights for leaves and stems plus petioles were determined after oven drying at 70°C for 48 h.

Growth analysis requires the determination of specific time intervals between successive plant harvests. Growth analysis is often conducted for plants grown in growth chambers where environmental variables are controlled and chronological time is easily determined. Because of the different planting dates, air temperatures inside the greenhouse varied among the four experiments. There were also some differences among the experiments in the specific chronological timing for the three destructive harvests. Differences in plant growth and development due to temperature or harvest timing were accounted for by use of growing degree days or thermal units (Tu) substituted for chronological time. Thermal units were calculated as:

$$Tu = (T_{max} + T_{min})/2 - T_b, \quad [1]$$

where T_{max} and T_{min} are the maximum and minimum daily air temperatures, respectively, and T_b is the base temperature considered here to be 15.5°C. Accumulated thermal units (ΣTu) were then summed over the time intervals of interest (Table 1).

Growth analysis was used to examine patterns of biomass loss and regrowth among the cultivars and sand abrasion treatments. Relative growth rate was calculated as

$$RGR = [\overline{\ln(M_2)} - \overline{\ln(M_1)}]/(\Sigma Tu_2 - \Sigma Tu_1), \quad [2]$$

where $\overline{\ln(M_2)}$ and $\overline{\ln(M_1)}$ are the mean ln-transformed shoot dry masses (Hoffmann and Poorter, 2002) at thermal times ΣTu_2 and ΣTu_1. Net assimilation rate was calculated as

$$NAR = (M_2 - M_1)/(\Sigma Tu_2 - \Sigma Tu_1) \times \{[\overline{\ln(A_2)} - \overline{\ln(A_1)}]/(A_2 - A_1)\}, \quad [3]$$

where A_2 and A_1 are total leaf area at thermal times ΣTu_2 and ΣTu_1. Leaf area ratio was calculated as:

$$LAR = 0.5 \times [(A_1/M_1) + (A_2/M_2)]. \quad [4]$$

The data were pooled for each of the four experiments. The four experiments were then treated as replicates, and data analysis and mean separation was performed using the MIXED procedure provided by the SAS Institute (SAS Institute, 1990). Regression analysis was used to describe the trends in shoot biomass, RGR and NAR with treatment time.

RESULTS

Figure 1 shows examples of plants subjected to the six sand abrasion treatment times. Total shoot biomass

Table 1. Greenhouse planting dates; sand abrasion treatment dates; dates for the first, second, and third destructive samplings; and chronological and thermal time intervals between the first and second destructive sampling date (Interval 1) and the second and third sampling dates (Interval 2).

Exp.	Planting date	Sand abrasion treatment date	First sample	Second sample	Third sample	Interval 1	Interval 2	Interval 1 ΣTu†	Interval 2, ΣTu
						d		°C d	
1	4 Oct. 2004	26–28 Oct. 2004	26 Oct. 2004	10 Nov. 2004	24 Nov. 2004	11–13	14	157–177	171
2	30 Nov. 2004	3–5 Jan. 2005	5 Jan. 2005	18 Jan. 2005	1 Feb. 2005	11–13	14	168–192	177
3	6 Sept. 2005	26–28 Sept. 2005	26 Sept. 2005	12 Oct. 2005	25 Oct. 2005	14–16	13	197–226	186
4	26 Oct. 2005	16–18 Nov. 2005	16 Nov. 2005	2 Dec. 2005	16 Dec. 2005	14–16	14	186–210	180

† ΣTu, accumulated thermal units.

Fig. 1. Examples of plant damage for cotton (cv. FM 5013) exposed to six sand abrasion treatments (0, 5, 10, 20, 30, and 40 min, left to right) on 21 Nov. 2005, ≈3 d following abrasion treatments.

plotted against sand abrasion treatment time for each of the three destructive samplings are shown in Fig. 2. Differences among cultivars and cultivar by treatment interactions were not significant for total shoot biomass ($P \leq 0.05$, data not shown). In general, shoot biomass averaged among cultivars was reduced with increasing sand abrasion treatment time for both the second and third destructive samples. Stem and leaf dry mass, leaf area, and final number of mainstem nodes are shown in Table 2. Stem dry mass and final node numbers were not different among the three cultivars, while there were differences among the three cultivars in leaf mass for the second destructive harvest. Cultivar effects for leaf mass in the third sample and leaf area in the second and third sampling were not different at $P \leq 0.05$. All measured plant parameters tended to be reduced with increasing sand abrasion treatment time except for final mainstem node numbers, which were increased by nearly one node per mainstem across the 0- to 40-min treatments.

The data in Fig. 2 and Table 2 were used to calculate RGR, NAR, and LAR for the two harvest intervals. Cultivar and cultivar × treatment interactions were not different for RGR, NAR, or LAR for either harvest interval (data not shown). Shown in Fig. 3 are RGR and NAR averaged across cultivars and plotted against treatment time for both the first and second harvest intervals. The LAR was not plotted in Fig. 3 because it was not significantly affected by treatment time. With increasing treatment time, RGR and NAR decreased in the first harvest interval but were increased in the second harvest interval. The LAR was not affected by treatment time in either harvest interval (data not shown). The NAR described about 82% of the variability in RGR indicating a linear relationship (Fig. 4).

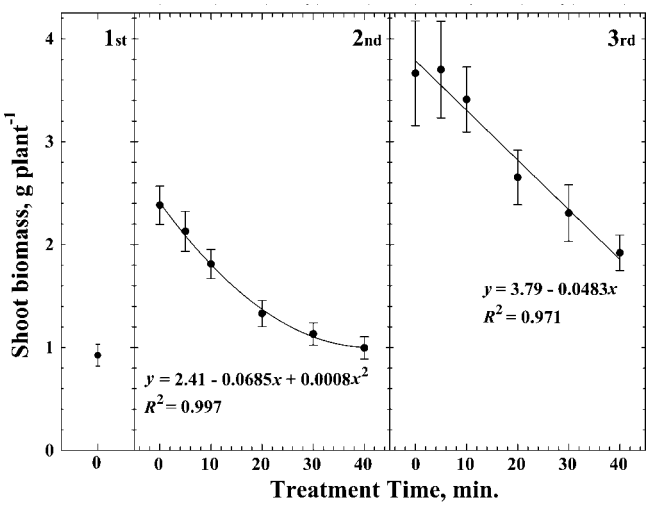

Fig. 2. Shoot biomass at three destructive harvests (first, second, and third) vs. six sand abrasion treatment durations averaged across three cotton cultivars. Means with the same letter are not significantly different at $P < 0.05$.

DISCUSSION

Biomass Accumulation

Immediately following the sand abrasion treatment and with increasing treatment time, leaves on the plants became increasingly wilted and dark necrotic spots began to appear on both leaves and stems. In the days following the treatment, damaged leaves began to exhibit completely desiccated areas and many of the more heavily damaged leaves were ultimately shed from the plant. The reduction in biomass with increasing treatment time (Fig. 2) is likely associated with both the loss of leaf biomass and a reduction in leaf area and assimilates. Compared with untreated controls, reductions in shoot biomass across the range in treatment times amounted to about 58% (Fig. 2, second sampling) and 48% (Fig. 2, third sampling) for the first and second harvest intervals, respectively, suggesting that differences in regrowth among the treatment times were beginning to diminish by the second harvest interval.

It is conceivable that gross morphological trait differences (e.g., okra leaf vs. normal leaf shape or glabrous vs. hairy epidermis) among cotton cultivars could lend themselves to increased resistance to sand abrasion. The cultivar FM 832 has an okra leaf shape while the other two cultivars have a normal leaf shape. In the second and third sampling, FM 832 leaf biomass and leaf area were not different compared with the other two cultivars. This suggests that the okra leaf shape did not provide additional resistance to sand abrasion or promote regrowth (Table 2).

During the second harvest interval, and with increasing treatment time, damaged plants responded by growing new leaves on lateral meristems. Most of this growth was on mainstem nodes where previously damaged leaves had been shed, giving these plants a more bushy appearance compared with untreated controls. Similarly, Fryrear (1971) reported that plants surviving the sand abrasion treatments were shorter than

Table 2. Stem and leaf dry mass, leaf area, and final number of mainstem nodes for the first, second, and third destructive sampling dates for three cultivars of cotton and six sand abrasion treatment durations.

	Stem dry mass			Leaf dry mass			Leaf area			No. nodes
	First	Second	Third	First	Second	Third	First	Second	Third	Third
	g						cm^2 $plant^{-1}$			
Cultivar										
FM 832	0.3a†	0.5a	1.2a	0.6a	0.8a	1.4a	112a	131a	196a	8.0a
FM 989	0.4a	0.7a	1.3a	0.7a	1.0ab	1.4a	130a	142a	201a	7.6a
FM 5013	0.3a	0.7a	1.5a	0.6a	1.1b	1.8a	133a	170a	251a	7.9a
Treatment duration, min										
0	0.3	0.9a	1.7a	0.6	1.5a	1.9a	125	231a	288a	7.3c
5		0.8ab	1.7a		1.3ab	1.9a		187ab	252ab	7.6bc
10		0.7abc	1.6ab		1.1abc	1.8ab		165abc	237ab	7.8abc
20		0.5bc	1.2ab		0.8bc	1.5ab		125bc	201ab	8.3a
30		0.5c	1.0ab		0.7c	1.3ab		98c	162ab	8.0ab
40		0.4c	0.9b		0.6c	1.1b		82c	154b	8.2a
					$P > F$					
Cultivar (C)	0.6830	0.1356	0.3128	0.7677	0.0232	0.0586	0.5970	0.0645	0.0512	0.3119
Treatment (T)		0.0010	0.0098		0.0003	0.0170		0.0005	0.0251	0.0007
C × T		0.6106	0.9423		0.4420	0.9966		0.3201	0.9823	0.2262

† Means within the same column and followed by the same letter are not significantly different at $P \leq 0.05$.

untreated controls but had more leaf area per unit of plant height. In the present study, leaf area regrowth of damaged plants was the result of both increases in lateral branch formation as well as an acceleration in the rate of mainstem node formation (Table 2). This increase in lateral branch formation of abraded plants may increase the sink demand for assimilates in the plant.

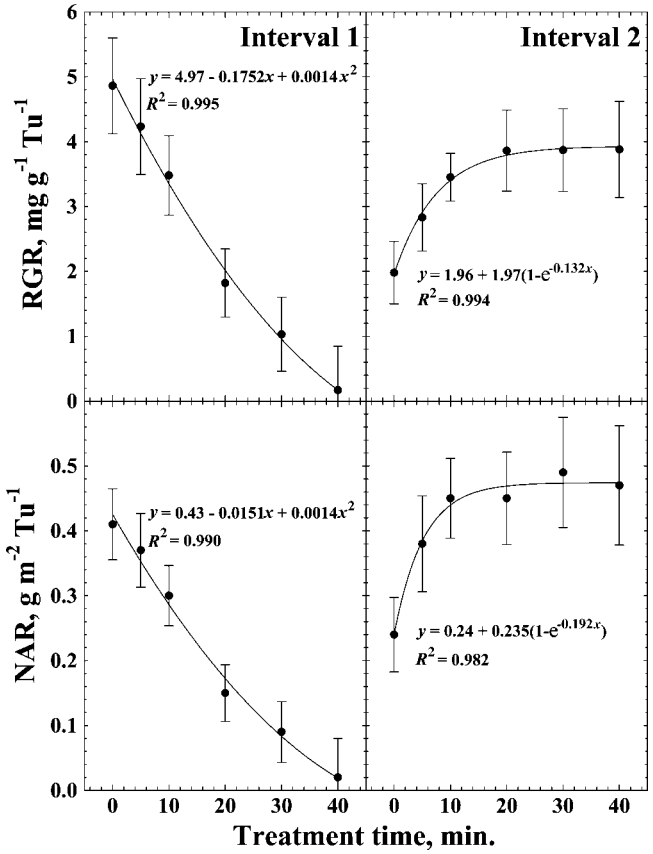

Fig. 3. Relative growth rate (RGR) and net assimilation rate (NAR) averaged across three cotton cultivars vs. six sand abrasion treatment durations for two growth intervals. Error bars are ± SE.

Growth Analysis

The RGR of untreated controls, treatment time zero, decreased from the first to the second harvest intervals (Fig. 3). The RGR can also be expected to vary across diurnal time intervals, becoming negative at night due to respiratory losses.

The LAR is a morphological trait, whereas NAR is a physiological trait. Since RGR is the product of NAR and LAR, growth rate is dependent on leaf area as well as average net assimilation on a leaf area basis. Reductions in RGR and NAR with increasing treatment time in the first harvest interval (Fig. 3) may be attributed to losses in leaf biomass and a reduction in both light interception and photosynthetic capacity of damaged leaves. In the second harvest interval, the increase in RGR and NAR with increasing treatment time, and the dependence of RGR on NAR rather than LAR is less easily explained in light of the findings of Poorter (1989). Reviewing 60 prior publications, Poorter (1989)

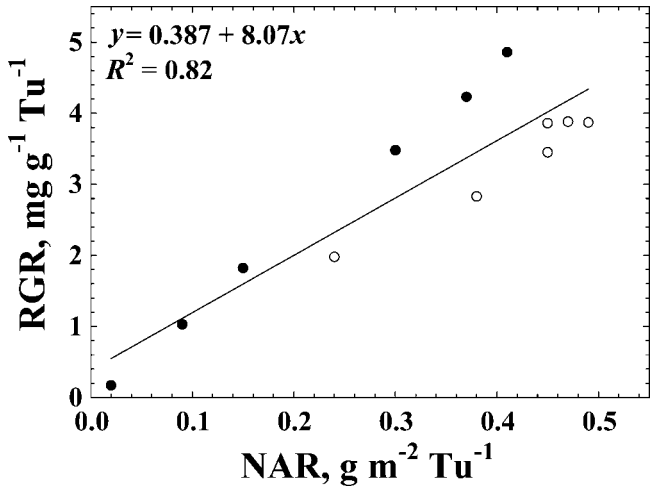

Fig. 4. Mean net assimilation rate (NAR) vs. mean relative growth rate (RGR) averaged across three cotton cultivars for cotton seedlings exposed to six sand abrasion treatment times. Closed and open symbols are for the first and second harvest intervals, respectively.

concluded that differences in RGR were largely caused by differences in LAR, with NAR of only secondary importance. Similarly, Poorter et al. (1990) concluded that differences in RGR among species was not caused by differences in the rate of photosynthesis per unit leaf area but by differences in the amount of physiologically active leaf area per unit plant mass (e.g., LAR). On the other hand, Villar et al. (2005) found that under the fluctuating field environment, the relative importance of NAR vs. LAR in determining RGR depended on the time frame under consideration. The NAR predominated during short time intervals while LAR became more important during longer time intervals. This was attributed to NAR being sensitive to short-term environmental fluctuations (e.g., light, temperature). During longer time intervals the plant integrates environmental variability, and so morphological features such as LAR predominately determine RGR. The greenhouse environment in the present experiments, with fluctuating temperatures and light levels, resembled the field environments described by Villar et al. (2005) rather than the growth chamber experiments described by Poorter (1989). Considering the effects of the sand abrasion treatments described here, NAR is the major determinant of RGR.

Wind and sand abrasion damage often reduce growth and photosynthesis compared with untreated controls (Armbrust et al., 1974; Armbrust, 1982; Michels et al., 1995). In this experiment, increasing treatment time reduced shoot biomass compared with untreated controls (Fig. 2). Relative biomass accumulation (RGR, Fig. 3) was increased with treatment time during the second harvest interval (Fig. 3). In previous sand abrasion studies, small amounts of sand blast injury actually resulted in increased shoot biomass compared with untreated controls for cotton, wheat (*Triticum aestivum* L.), and sorghum [*Sorghum bicolor* (L.) Moench] (Armbrust, 1968, 1982; Armbrust et al., 1974). When measured on a per-pot basis, whole-plant photosynthesis was reduced by sand abrasion, but when expressed on a live-leaf area basis, photosynthesis increased by 8 to 18% in wheat (Armbrust et al., 1974) and 48 to 85% in sorghum (Armbrust, 1982). These increases in photosynthesis expressed on a leaf area basis of abrasion damaged plants suggest that NAR may have also been increased in those experiments.

In their review of the literature, Poorter and Nagel (2000) describe the allocation of biomass between roots and shoots in plants, such that root–shoot biomass ratio is very rapidly restored following the pruning of a large fraction of roots or leaves. In this experiment, root biomass was not measured, so the potential contribution of remobilized assimilate from the roots to shoots could not be assessed. Future research at this location will focus on the relative contributions of remobilization of root mass to the shoots vs. potentially enhanced photosynthetic rates in restoring leaf area in sand blast damaged cotton plants. There is a need to identify physiological or morphological traits that provide resistance to sand abrasion and enhanced recovery of damaged plants.

CONCLUSIONS

Wind blown sand abrasion initially reduced leaf area, shoot biomass, RGR, and NAR. During the recovery phase or the second harvest interval, both RGR and NAR increased with increasing treatment time, reflecting increased shoot growth efficiency of previously damaged plants. In both harvest intervals, RGR was determined largely by NAR rather than LAR. Plants in the 40-min treatment duration survived and recovered during the second harvest interval, indicating that surviving but completely defoliated cotton plants in the field may not require replanting.

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REFERENCES

Adriano, D.C., D.V. Armbrust, and L.S. Murphy. 1969. Foliar absorption of urea by sandblasted wheat seedlings. Agron. J. 61: 575–576.

Armbrust, D.V. 1968. Windblown sand abrasive injury to cotton plants. Agron. J. 60:622–625.

Armbrust, D.V. 1972. Recovery and nutrient content of sandblasted soybean seedlings. Agron. J. 64:707–708.

Armbrust, D.V. 1979. Wind and sandblast damage to tobacco plants at various growth stages. Tob. Sci. 23:117–119.

Armbrust, D.V. 1982. Physiological responses to wind and sandblast by grain sorghum plants. Agron. J. 74:133–135.

Armbrust, D.V. 1984. Wind and sandblast injury to field crops: Effect of plant age. Agron. J. 76:991–993.

Armbrust, D.V., J.D. Dickerson, and J.K. Greig. 1969. Effect of soil moisture on the recovery of sandblasted tomato seedlings. J. Am. Soc. Hortic. Sci. 94:214–217.

Armbrust, D.V., G.M. Paulsen, and R. Ellis, Jr. 1974. Physiological responses to wind- and sandblast-damaged winter wheat plants. Agron. J. 66:421–423.

Downes, J.D., D.W. Fryrear, R.L. Wilson, and C.M. Sabota. 1977. Influence of wind erosion on growing plants. Trans. ASAE 20:885–889.

Fryrear, D.W. 1971. Survival and growth of cotton plants damaged by windblown sand. Agron. J. 63:638–642.

Fryrear, D.W. 1973. Wind damage. . .Should I replant? American Cotton Grower May:21–25.

Fryrear, D.W. 1986. Wind erosion and its effects on plant growth. Ann. Arid Zone 25(4):245–254.

Fryrear, D.W., D.V. Armbrust, and J.D. Downes. 1975. Plant response to wind erosion damage. Land use: Food and living. Proc. 30th Ann. Meeting of the Soil Conservation Soc. of Am., San Antonio, TX. 10–13 Aug. 1975. SCSA, Des Moines, IA.

Fryrear, D.W., and J.D. Downes. 1975. Estimating seedling survival from wind erosion parameters. Trans. ASAE 18:888–891.

Fryrear, D.W., J. Stubbendieck, and W.G. McCully. 1973. Grass seedling response to wind and windblown sand. Crop Sci. 13:622–625.

Grace, J. 1977. Plant responses to wind. Academic Press, London.

Hoffmann, W.A., and H. Poorter. 2002. Avoiding bias in calculation of relative growth rate. Ann. Bot. (London) 80:37–42.

Lyles, L., and N.P. Woodruff. 1960. Abrasive action of windblown soil on plant seedlings. Agron. J. 52:533–536.

Merrill, S.D., A.L. Black, D.W. Fryrear, A. Saleh, T.M. Zobeck, A.D. Halvorson, and D.L. Tanaka. 1999. Soil wind erosion hazard of spring wheat-fallow as affected by long-term climate and tillage. Soil Sci. Soc. Am. J. 63:1768–1777.

Michels, K., D.V. Armbrust, B.E. Allison, and M.V.K. Sivakumar. 1995. Wind and windblown sand damage to pearl millet. Agron. J. 87:620–626.

Poorter, H. 1989. Interspecific variation in relative growth rate: On ecological causes and physiological consequences. p. 45–68. *In* H. Lambers et al. (ed.) Causes and consequences of variation in

growth rate and productivity of higher plants. SPB Academic Publ., The Hague, the Netherlands.
Poorter, H., and O. Nagel. 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO_2, nutrients and water: A quantitative review. Aust. J. Plant Physiol. 27: 595–607.
Poorter, H., C. Remkes, and H. Lambers. 1990. Carbon and nitrogen economy of 24 wild species differing in relative growth rate. Plant Physiol. 94:621–627.
SAS Institute. 1990. SAS/STAT users guide. v. 6, 4th ed., Vol. 2. SAS Inst., Cary, NC.
Skidmore, E.L. 1966. Wind and sandblast injury to seedling green beans. Agron. J. 58:311–315.
Stout, J.E., and T.M. Zobeck. 1997. Intermittent saltation. Sedimentology 44:959–970.
Villar, R., T. Maranon, J.L. Quero, P. Panadero, F. Arenas, and H. Lambers. 2005. Variation in relative growth rate of 20 *Aegilops* species (Poaceae) in the field: The importance of net assimilation rate or specific leaf area depends on the time scale. Plant Soil 272:11–27.
Zobeck, T.M., and R.S. Van Pelt. 2006. Wind-induced dust generation and transport mechanics on a bare agricultural field. J. Hazard. Mater. 132:26–38.